The surface accumulation of larval fishes by hydrodynamic convergence within the Mississippi River plume front

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Abstract—In September 1987 and May 1988 densities of larval fishes at the surface were greater within the frontal zone of the Mississippi River plume than they were in plume or shelf waters. Sharp turbidity discontinuities of 10–50 m width accompanied by temperature and salinity discontinuities were embedded within this large-scale frontal zone, which itself spanned 2–20 km. Apparent convergent motion normal to turbidity discontinuities had velocities in the range of 0–0.8 m s^{-1}: lateral shear was also evident. Exceptionally high densities of larval fishes were not always observed at turbidity discontinuities. Turbidity discontinuities, often sinuous in configuration, formed and dissipated over time scales of 2–6 h. Expected densities of larval fishes within frontal convergence zones, calculated with a simplified advection–diffusion model, approximated mean and median densities observed within the large-scale frontal zone.

INTRODUCTION

HYDRODYNAMIC convergence has been used to explain the accumulation of larval fishes within the frontal zone of the Mississippi River plume in the northern Gulf of Mexico (GOVONI *et al.*, 1989) and the Rhône River plume in the western Mediterranean (SABATÉS, 1990). In the Gulf of Mexico, larval gulf menhaden, *Brevoortia patronus*, occurred in inordinately high densities at the surface along turbidity discontinuities during winter, when the Mississippi River plume was well defined as a thin lens of cold, turbid, low-salinity water projecting over the warmer, saltier shelf waters in the northern Gulf (GOVONI *et al.*, 1989). In this study, densities of larvae were highly variable; i.e. exceptionally high densities were not evident everywhere along these turbidity discontinuities. The movement of flotsam toward, and its accumulation at, the frontal interface indicated convergence of surface water, but no direct observations of convergent velocities attendant with estimates of larval fish density were available. The strength of convergence was indexed instead with a simple formulation that was based upon the density difference between the plume and shelf waters, but derived values were not correlated with densities of larval fishes. Frontal convergence, as a mechanism that accumulates larval fishes, was consequently viewed as a localized and complex condition. This perception, lacking in observational detail on the vertical and horizontal structure of the frontal zone and the kinematics of frontal convergence, is vague. SABATÉS (1990) similarly used frontal

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convergence to explain the aggregated distribution of larval fishes at the riverine plume front without details of the physics of the frontal zone.

While riverine and estuarine plume fronts have been well studied from the physical perspective (see reviews in BOWMAN and IVERSON, 1978), recent work has shown that the physical behavior of plumes and their associated frontal zones can differ among plumes of differing spatial scales (CURTIN and LEGECKIS, 1986; CURTIN, 1986a, 1986b; GARVINE, 1986; LUKETINA and IMBERGER, 1989; O'DONNEL, 1990). In common with other riverine plumes, the Mississippi River plume exhibits small-scale turbidity discontinuities, but unlike many smaller plumes (GARVINE, 1987), it is acted upon by Coriolis (WRIGHT and COLEMAN, 1971).

Here we examine the surface distribution of larval fishes about the Mississippi River plume in autumn and spring, when riverine discharge is seasonally minimal and maximal (DINNELL and WISEMAN, 1986). We then compare the density of surface dwelling larval fishes within the plume's frontal zone with concomitant estimates of the velocity of frontal convergence. Finally, we compare observed densities of larval fishes within the frontal zone with expected densities calculated with a simplified version of the model of OLSON and BACKUS (1985), a model that describes the concentrating of depth-keeping fishes at fronts in a simplified convergent flow field. The purpose of this later objective is to determine if convergence can account for observed densities of fish larvae.

METHODS

Because frontal convergence (GARVINE, 1977) and the accumulation of larval fishes (GOVONI et al., 1989) is a surface phenomenon, we examined the distribution of surface dwelling fish larvae as observed in neuston collections. We collected ichthyoneuston in and about the Mississippi plume front with a 1 by 2 m neuston net fitted with a 947 μm mesh net towed for 10 min at 1.8 km h^{-1} and measured the velocity of frontal convergence on two cruises: in September 1987 and in May 1988. The neuston net sampled the upper 0.5 m of the water column. Stations allocated at approximate 5 km intervals along transects approximately normal to the Mississippi Delta were occupied once on each cruise (Fig. 1). Hydrographic profiles of the water column (temperature and salinity) were obtained electronically at each station along with collections of ichthyoneuston. Stations were occupied in serial fashion regardless of tidal phase or time of day. Each transect required approximately 12 h to complete.

We estimated convergent velocities at positions where the plume's turbidity discontinuities, evidenced by sharp color and textural discontinuities of the sea-surface, coincided with temperature and salinity discontinuities. One of these discontinuities was encountered within a transect, while six others were encountered between transects (Fig. 1).

At turbidity discontinuities, colored surface drifters (computer cards) were released along short transects that perpendicularly traversed the frontal interface from 185 to 500 m on either side (e.g. red drifters in plume water, white at the frontal interface, and blue in shelf waters). Preliminary work with both surface drifters and surface-water drogues in July 1987 indicated that surface drifters were more responsive to the movement of shallow plume water and that neither drifters nor drogues responded beyond 500 m perpendicular to the frontal interface. Positions that marked the beginning and end of the line of drifters, as well as the position of the frontal interface, were recorded on a Loran-C plotter. The elapsed time from the release of drifters farthest away from the turbidity discontinuity
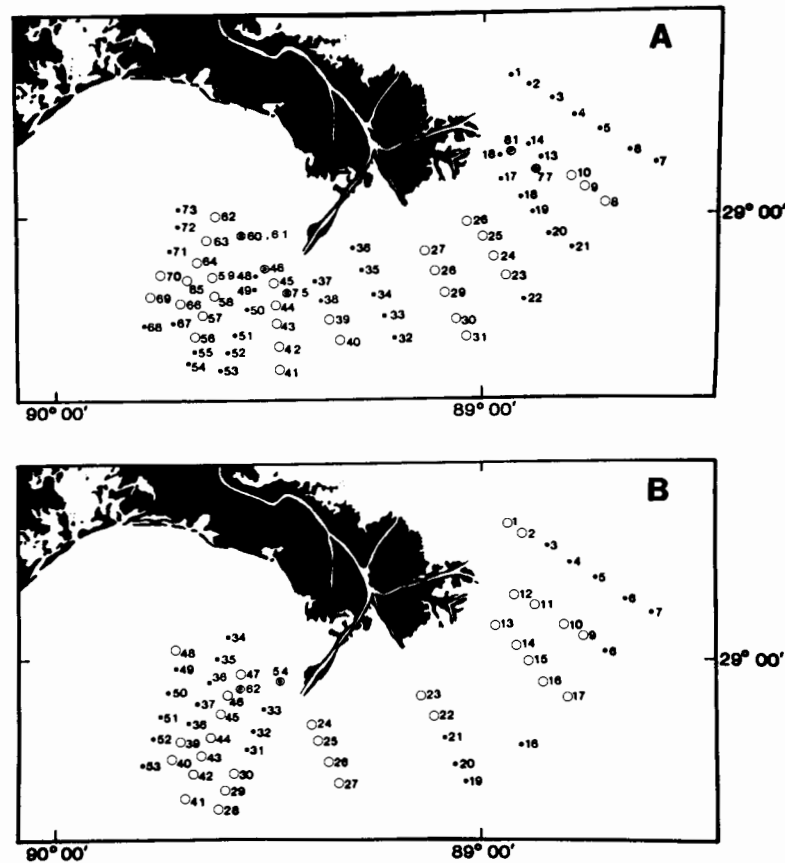
Fig. 1. Stations occupied in and about the Mississippi River plume (open symbols denote stations occupied during the day, closed symbols denote stations occupied during the night, and encircled symbols denote locations of turbidity discontinuities where convergence was measured): A—September 1987; B—May 1988.

until their alignment along the frontal interface was used with distance, as measured by the difference between positions, to estimate the velocity of apparent frontal convergence (i.e. observations were Lagrangian).

We employed the advection–diffusion model of OLSON and BACKUS (1985) to calculate expected densities of larval fishes at the plume front. This model assumes that larval fishes disperse and swim randomly in the horizontal, but sense and counter vertical motion. As a result, vertical advection and diffusion is ignored. It also assumes that diffusivities along (the y-coordinate) and normal to the frontal interface (the x-coordinate) are equivalent. If one assumes further that observations were made when the distribution of larval fishes was stable, i.e. at steady-state, then the Olson and Backus model takes the form

$$C = C_0 \frac{1}{[(2k/(-V/L)\alpha_0]^{1/2}} \exp\left(\frac{-V}{\dfrac{L}{2K}} X^{1/2} - \alpha_0 Z^2 \right)$$
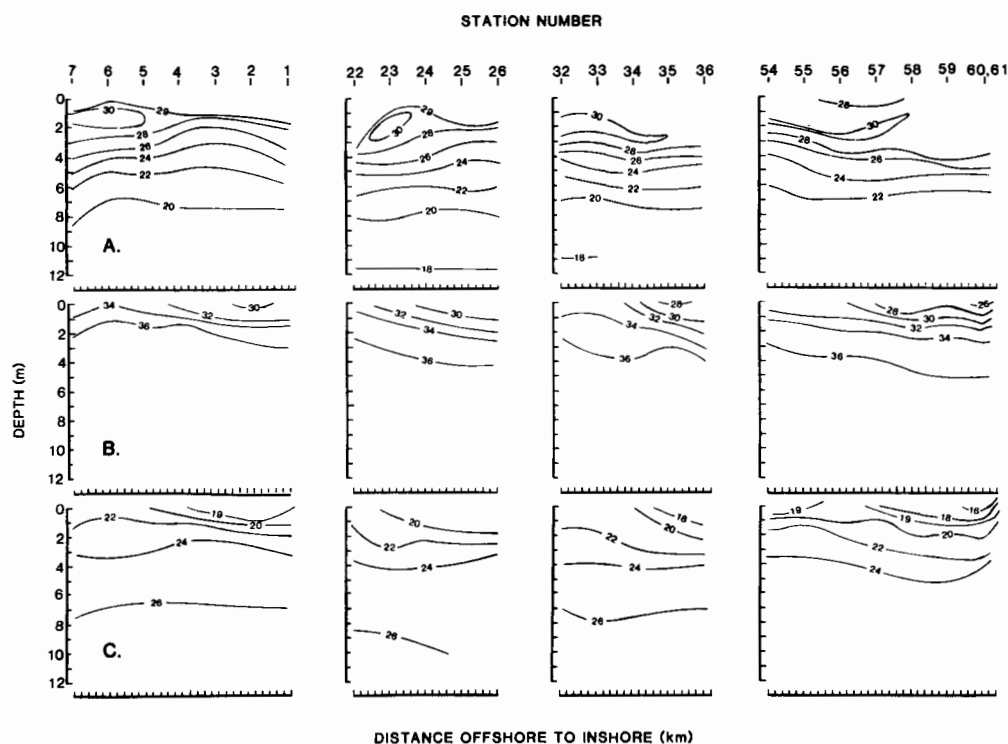
STATION NUMBER

Fig. 2.   Selected hydrographic sections across the Mississippi River plume in September 1987:
A—temperature; B—salinity; C—density (σ_t).

where C_0 is the observed median density of larval fishes in plume and shelf waters, i.e. outside of the frontal zone (number of larvae $\times 10^3 \ \mathrm{m}^{-2}$), K is the horizontal diffusivity coefficient in the x-coordinate ($\mathrm{m}^2\,\mathrm{s}^{-1}$), V is observed convergent velocity ($\mathrm{m\,s}^{-1}$), L is the length scale of convergence (500 m), a_0 is the inverse square of the length scale, X, associated with horizontal distance away from the front (m^{-1}), and Z is the depth at the frontal interface (m). If interest is only in the maximum density of fishes at the surface near the frontal interface, then

$$C = C_0 \left(\frac{VL}{2K}\right)^{1/2}.$$

All parameter estimates were empirical except K, the diffusivity coefficient. Diffusivity is spatially and temporally scale dependent (MURTHY, 1976; OKUBO, 1976). LAPICQUE and BREITTMEYER (1973; in LEWIS, 1984) estimated the diffusivity of passive particles perpendicular to the frontal interface of riverine plumes to be in the range of 2–10 $\mathrm{m}^2\,\mathrm{s}^{-1}$. Because of the apparently narrow width of convergence zones, diffusivity was allowed to vary from 1 to 10 $\mathrm{m}^2\,\mathrm{s}^{-1}$ in our calculations of expected densities.

RESULTS

In September 1987 the plume was a thin (1–4 m) surface lens of turbid, warm, low-salinity water that overlay the clear, cool, high-salinity shelf waters (Fig. 2). In May
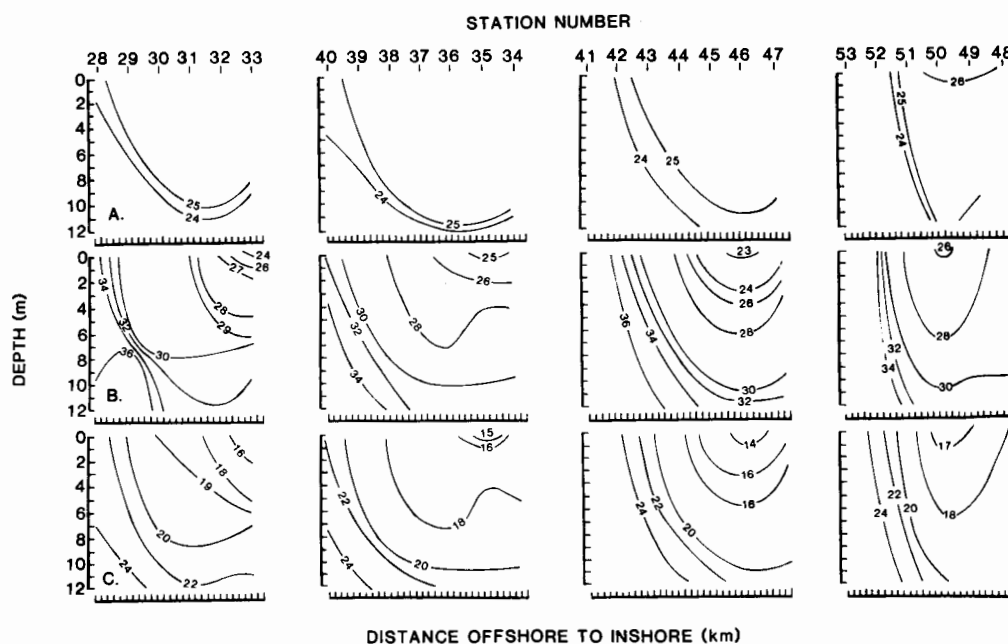
STATION NUMBER

Fig. 3. Selected hydrographic sections across the Mississippi River plume in May 1988: A—temperature; B—salinity; C—density (σ_t).

1988, when discharge from the Mississippi River is greatest, warm and freshened plume water occupied the water column down to 12 m or more (Fig. 3). Temperature and salinity differences between plume and shelf waters were greater in spring than in autumn. In either season, plume water was horizontally separated from ambient shelf waters by a frontal zone evidenced by the horizontal compression and surface-intersection of the same isopycnals that constitute the depth-discontinuity layer beneath the plume (*sensu* GARVINE, 1987). We defined the large-scale frontal zone as encompassing those adjacent stations within a transect that differed in surface density by >1 σ_t value (Fig. 4). So defined, this large-scale frontal zone spanned from 2 to 20 km (Fig. 5).

Embedded within this large-scale frontal zone, were small-scale, ephemeral turbidity discontinuities, characterized by marked contrasts in sea-surface color and texture with accompanying foam and flotsam rows. These discontinuities were encountered on five dates in September 1987, two in May 1988 (Table 1). Turbidity discontinuities usually lay near the inshore margin of the frontal zone, but they were not apparent everywhere within this zone (Fig. 4). The spatial scale of turbidity discontinuities ranged from 10 to 50 m (normal to the interface). These fronts had temperature, salinity, and σ_t discontinuities that ranged from 0.107 to 1.293 $\Delta°C$, 0.643 to 4.237 $\Delta‰$, and 0.433 to 3.247 $\Delta\sigma_t$ for the upper 0.5 m of water (Table 1). The interface of turbidity discontinuities was often sinuous, and on occasion, secondary lines of color and sea-surface texture were observed parallel to, or intersecting, the primary front. Turbidity discontinuities appeared to form and dissipate over a period of 2–6 h.

Surface drifters typically moved from both sides of turbidity discontinuities toward, then
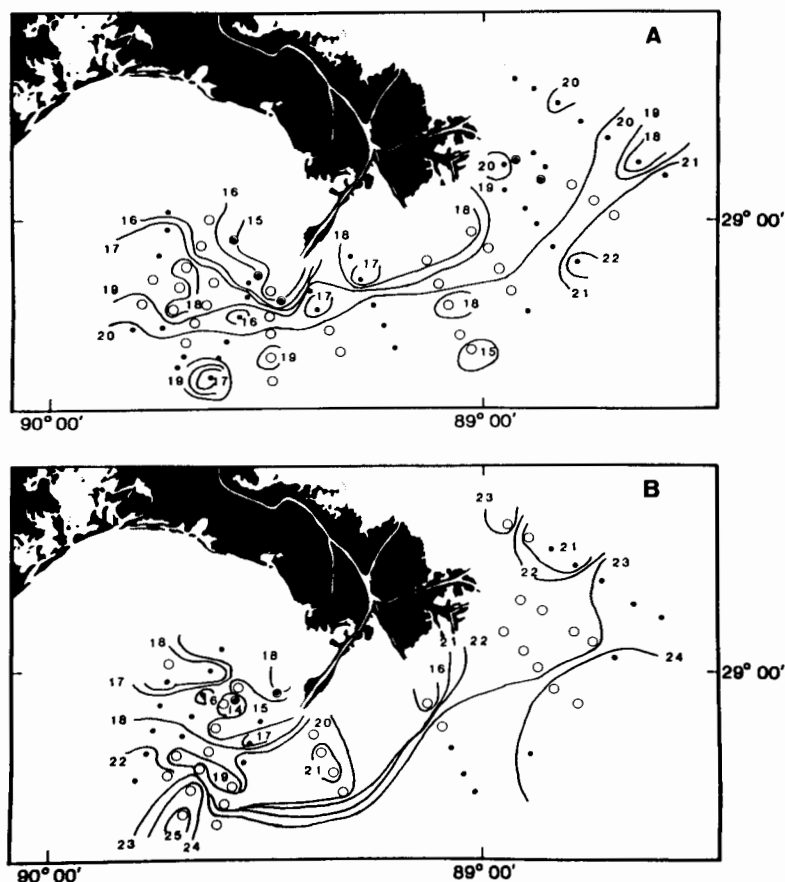
Fig. 4. Plan view of surface isopycnals in and about the Mississippi River plume (open symbols denote stations occupied during the day, closed symbols denote stations occupied during the night, and encircled symbols denote locations of turbidity discontinuities): A—September 1987; B—May 1988.

aligned laterally along the interface. The alignment of surface drifters along the interface indicated the presence of lateral shear.

Apparent convergent velocities differed between plume water and shelf waters, and at some fronts, drifters released in either plume or shelf waters did not move toward the interface at all (Table 1). Apparent convergent velocities on both sides of the interface ranged from 0 to 0.8 m s^{-1}, but showed no consistent pattern with the difference in water density across turbidity discontinuities. Overall, movement of surface drifters toward the interface was faster in shelf waters than it was in plume water; the fronts observed on 31 May 1988 were exceptions (Table 1). Averaged for both sides of the frontal interface, velocities ranged from 0.05 to 0.25 m s^{-1} in September 1987 and from 0.15 to 0.40 m s^{-1} in May 1988.

Frequency distributions of the larval fish densities were highly skewed and kurtotic (skewness and kurtosis = 3.20 and 13.65 in September 1987; 1.78 and 2.09 in May 1988)
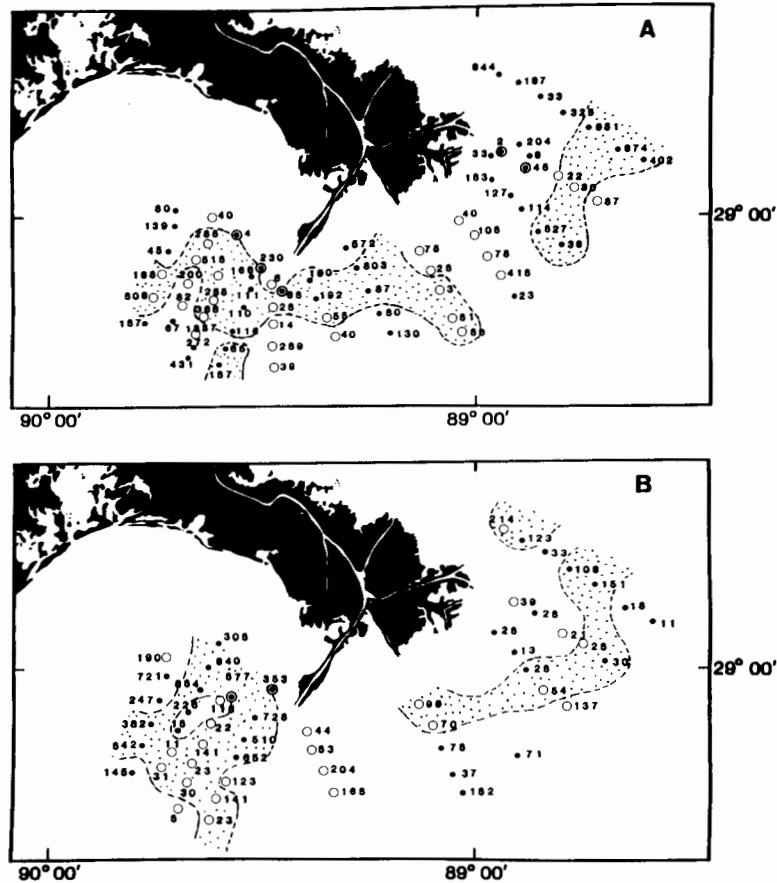
Fig. 5. The spatial distribution of larval fishes in and about the Mississippi River plume frontal zone (stippled areas indicate the plume's frontal zone, open symbols denote stations occupied during the day, closed symbols denote stations occupied during the night, and encircled symbols indicate locations of turbidity discontinuities). Numbers are densities of larval fishes (number $\times$ 10^3 m^{-2}): A—September 1987; B—May 1988.

and did not conform with a random normal distribution ($P < 0.05$: analysis of variance for normality (SHAPIRO and WILK, 1965)). Means were greater than median densities (Fig. 6).

If frontal convergence operates to accumulate larval fishes, densities should be greater within the frontal zone than in shelf or plume waters. Frontal convergence is a surface phenomenon, however, and larval fishes typically disperse from the surface layer by day (NEILSON and PERRY, 1990), possibly producing diel differences in the action of surface convergence on their distribution. Mean and median densities of larval fishes at the surface were greatest at stations within the large-scale frontal zone when those stations were occupied during the night (Figs 5 and 6). In autumn, 11 of 16 densities that were above the 75th percentile for time of day (i.e. $>204 \times 10^3$ m^{-2} for stations occupied during the day and $>325 \times 10^3$ m^{-2} for stations occupied during the night) occurred within the frontal zone (Fig. 5A). In spring, 16 of 26 densities that were above the 75th percentile for time of

Table 1. *Physical characteristics of the small-scale front of the Mississippi River plume as observed at turbidity discontinuities*

| Date | Station number | Discontinuity | | | Convergent velocity of shelf water $(m s^{-1})$ | Convergent velocity of plume water $(m s^{-1})$ |
		ΔT (°C)	ΔS (‰)	$\Delta \sigma_t$		
5 Sept. 87	46	0.113	0.643	0.443	0.2	0.1
6 Sept. 87	60, 61	0.408	1.087	0.680	0.1	0.0
7 Sept. 87	75	0.112	2.779	2.036	0.5	0.0
8 Sept. 87	77	0.369	1.057	0.676	0.1	0.1
9 Sept. 87	81	0.283	4.237	3.247	0.2	0.0
31 May 88	54	0.107	0.532	0.433	0.0	0.8
31 May 88	62	1.293	4.234	3.017	0.0	0.3

day (i.e. $>137 \times 10^3$ m^{-2} for stations occupied during the day and $>51 \times 10^3$ m^{-2} for stations occupied during the night) did so (Fig. 5B). Exceptional densities did not occur regularly at turbidity discontinuities. One of five densities observed at turbidity discontinuities was above the 75th percentile in September 1987; one of two in May 1988 (Fig. 6). In September, this exceptional density (Sta. 46) occurred where convergent velocities were high, but not maximal, and were roughly similar on both sides of the discontinuity. In May, the exceptional density (Sta. 54) corresponded with the maximal convergent velocity observed (Table 1; Figs 1 and 5). The maximum density observed in this study, 1837 larvae $\times 10^3$ m^{-2} (Sta. 56, May 1987) occurred outside of the frontal zone as we defined it, but this density, nonetheless, was close by in an area of complex horizontal hydrographic
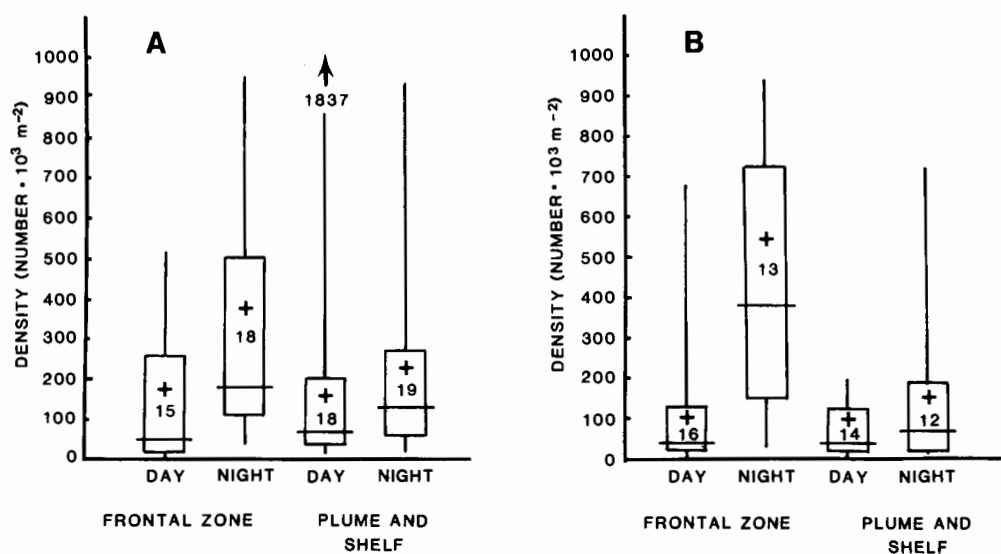

Fig. 6. Descriptive statistics of the density of fish larvae in and about the Mississippi River plume front. Boxes enclose interquartile ranges with the number of observations within, crosses depict means, horizontal slashes depict medians, and vertical lines ranges: A—September 1987; B—May 1988.
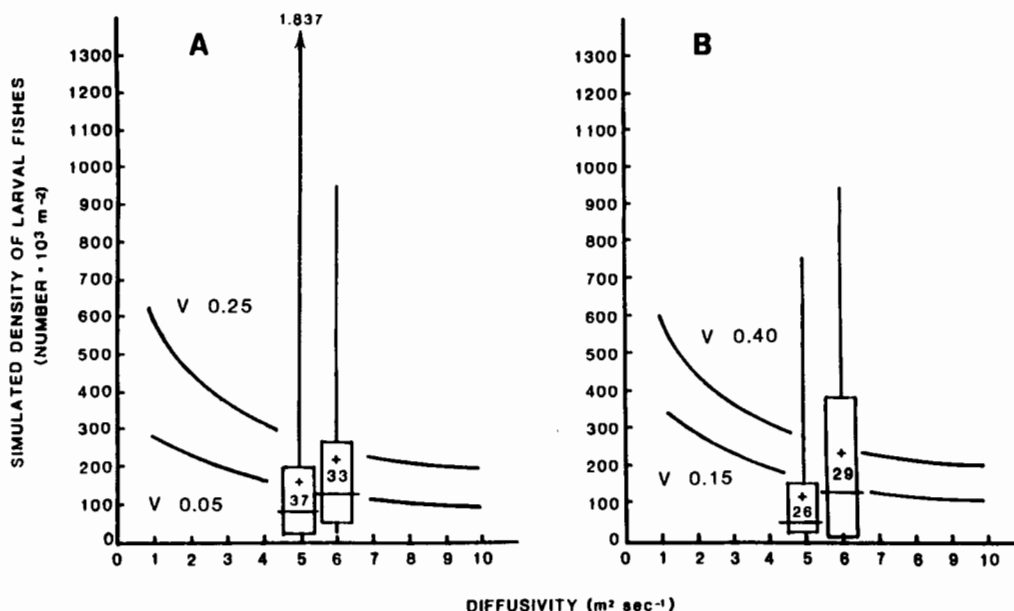
Fig. 7. The accumulation of larval fishes at the surface at the Mississippi River plume front. Solid curves depict expected calculated densities of larval fishes for the range of apparent convergent velocities (v) and median densities of larvae outside of the frontal zone (C_0), boxes enclose observed interquartile ranges in densities of larval fishes within the frontal zone by day (left) and night (right), numbers within boxes indicate the number of observations, crosses indicate means, horizontal slashes indicate medians, and vertical lines indicate ranges of densities: A—September 1987 ($C_0 = 82 \times 10^3 \, \mathrm{m}^{-2}$); B—May 1988 ($C_0 = 63 \times 10^3 \, \mathrm{m}^{-2}$).

structure (Figs 1, 2 and 4). Given the dynamic nature of the plume front, this exceptional density may be a remnant aggregation of larvae accumulated by frontal convergence, then advected away from the frontal zone by stirring.

Densities of larval fishes within the frontal zone are probably the result of their accumulation along ephemeral convergence zones and subsequent dispersal and mixing during relaxation of convergence. Expected densities of larval fishes calculated with the advection–diffusion model were within the range of observed densities within the large-scale frontal zone, given a length scale (L) of 500 m, background densities (C_0) of $82 \times 10^3 \, \mathrm{m}^{-2}$ in September 1987 and $62 \times 10^3 \, \mathrm{m}^{-2}$ in May 1988 (median densities of larval fishes observed in plume and shelf waters irrespective of time of day), and velocities (V) of 0.05–$0.25 \, \mathrm{m \, s}^{-1}$ in autumn and 0.15–$0.40 \, \mathrm{m \, s}^{-1}$ in spring (the end points of the range of convergent velocities averaged for both sides of the frontal interface). Ranges of expected densities overlapped the interquartile range of observed densities and lay close to mean and median densities, especially at diffusivity coefficient values above $5 \, \mathrm{m}^2 \, \mathrm{s}^{-1}$ (Fig. 7).

DISCUSSION

The Mississippi River plume shares some similarities with other riverine plumes. It is a buoyant plume with a large-scale frontal zone of complex horizontal hydrographic

structure where isopycnals characteristic of the depth discontinuity layer intersect the surface. Embedded within this large-scale frontal zone are small-scale turbidity disconti- nuities where convergence is often present. The large-scale front resembles the "degener- ate fronts" of the Connecticut River plume; small scale fronts resemble "boundary fronts" (Garvine, 1987). Current thought suggests that convergent motion of plume water results from spreading of plume water over ambient shelf waters as well as from the action of horizontal pressure gradient forces. As such, observed convergent motion of shelf waters is apparent, not real; i.e. shelf waters are overrun by and submerge under plume water (Garvine, 1987). The apparent velocities of convergence observed here, although somewhat higher, are of the same order of magnitude as those calculated by Govoni et al. (1989) under the assumption that convergence was driven in both plume and shelf waters by pressure gradient force. Observed convergent velocities also agree with those observed for the smaller Connecticut River (Garvine, 1977). The Mississippi River plume differs from other riverine plumes in other ways. Its larger scale subjects it to the influence of Coriolis force (Wright and Coleman, 1971), unlike the Connecticut River plume (Garvine, 1987). Its turbidity discontinuities are more often associated with the inshore margin of the plume rather than the offshore margin, as is typical of the Connecticut River plume (Garvine, 1987). In profile, it is deeper in the spring than other, smaller plumes. Also, it is deeper in spring than it is in autumn or winter (Govoni et al., 1989), owing to the vernal freshet (Gunter, 1979).

Our application of the advection–diffusion model is a highly simplified mechanistic representation that is based upon several assumptions. Densities of fish larvae simulated by the model depend most heavily on the assumed value of diffusivity, but there is some question concerning appropriate values for diffusivity within frontal zones. While the range of values assumed in our application seem appropriate for the spatial scale of observed convergence zones, Lewis (1984) suggested values of the order of 10–$100 \ m^2 \ s^{-1}$. Further, the model assumes that diffusivity is symmetrical in the x- and y-coordinates, but Lam et al. (1984) indicate that diffusion along the front may be much greater than it is across the front. With the simplified model, densities decline precipitously with diffusivity values $>1 \ m^2 \ s^{-1}$, and approach an asymptote with values above $>5 \ m^2 \ s^{-1}$ (Fig. 7). Another assumption of the model is that the population of larval fishes in and about the Mississippi River plume front is stable, i.e. that spawning of fishes within the frontal zone does not account for greater abundances of larvae there. Whereas there is evidence that some fishes, including members of the Engraulidae common to the Mississippi plume (Grimes and Finucane, 1991) spawn within frontal zones (Govoni, in press), the neuston net, with its $947 \ \mu m$ mesh, sampled only large larvae, not yolk-sac or small larvae, the products of recent spawning. Yet another assumption is that larval fishes have the capability of countering downward motion at the frontal interface. Within the context of Olson and Backus (1985), maximum downward motion is $\cong 3V/L$. Given the observed horizontal convergent velocities, downward motion should have ranged from 0.005 to $0.20 \ m \ s^{-1}$ at a depth of 5 m or less along the frontal interface, whereas sustained (as opposed to burst) swimming speeds of larval fishes range from 0.003 to 0.01 m s^{-1} (Bailey and Houde, 1989). To the extent that these ranges overlap, fish larvae should be capable of countering downward motion at the frontal interface some of the time. With our assumptions, expected densities of surface-dwelling larval fishes at the frontal interface, calculated with the advection–diffusion model, agree in the main with observed densities.

Frontal convergence can explain why densities of larval fishes were greater within the

frontal zone than they were in the adjacent plume or shelf waters, but it does not explain why exceptionally high densities were not evident everywhere within the frontal zone. The discontinuous distribution of larval fishes within the frontal zone is best explained by the ephemeral nature and the kinematic complexity of convergence zones associated with turbidity discontinuities. In winter, exceptional densities of larval fishes occurred in proximity (<100 m) of turbidity discontinuities (Govoni et al., 1989), but variation among serial, replicate surface samples taken along turbidity discontinuities in winter was high both at meter and kilometer scales. This variation is probably typical along these features, and may explain why exceptional densities were not observed in the few, single collections taken in autumn and spring (only two of seven single collections taken near these features in autumn and spring produced exceptional densities). Accumulation of larval fishes at the frontal interface is limited by the time scale within which convergence operates (the formation and dissipation of sharp, small-scale turbidity discontinuities) and is opposed by the dispersion of larvae away from the front. These physical features form during ebb tide and dissipate during flood tide: a 12 h diurnal tidal cycle prevails in the northern Gulf of Mexico (Seim et al., 1987). Dispersion within the large-scale front is effected by turbulence associated with the complexity of the front. For example, meanders and eddies that result from hydrodynamic instability are common attributes of riverine plume fronts (Simpson and James, 1986). From a ship's launch, one of us (J.J.G.) has also observed meter scale vertical mixing and horizontal eddies along turbidity discontinuities. The spatial distribution of larvae within the large-scale frontal zone is the aggregate result of the repeated formation and degeneration of convergence zones associated with small-scale turbidity discontinuities.

REFERENCES

Bailey K. M. and E. D. Houde (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, 25, 1–83.

Bowman M. J. and R. L. Iverson (1978) Estuarine and plume fronts. In: *Oceanic fronts in coastal processes*, M. J. Bowman and W. E. Esaias, editors, Springer-Verlag, New York, pp. 87–104.

Curtin T. B. (1986a) Physical observations in the plume region of the Amazon River during peak discharge—II. Water masses. *Continental Shelf Research*, 6, 56–71.

Curtin T. B. (1986b) Physical observations in the plume region of the Amazon River during peak discharge—III. Currents. *Continental Shelf Research*, 6, 73–86.

Curtin T. B. and R. V. Legeckis (1986) Physical observations in the plume region of the Amazon River during peak discharge—I. Surface variability. *Continental Shelf Research*, 6, 31–51.

Dinnell S. P. and W. J. Wiseman (1986) Fresh water on the Lousiana and Texas shelf. *Continental Shelf Research*, 6, 765–784.

Garvine R. W. (1977) Observations of the motion field of the Connecticut River plume. *Journal of Geophysical Research*, 82, 441–454.

Garvine R. W. (1986) The role of brackish plumes in open shelf waters. In: *The role of freshwater outflow in coastal marine ecosystems*, S. Skreslet, editor, Springer-Verlag, pp. 47–65.

Garvine R. W. (1987) Estuary plumes and fronts in shelf waters: a layer model. *Journal of Physical Oceanography*, 17, 1877–1896.

Govoni J. J., D. E. Hoss and D. R. Colby (1989) The spatial distribution of larval fishes about the Mississippi River plume. *Limnology and Oceanography*, 34, 178–187.

Govoni J. J. (In press) Flux of larval fishes across frontal boundaries: examples from the Mississippi River plume front and the western Gulf Stream front in winter. *Contributions in Science, Natural History Museum of Los Angeles.*

Grimes C. B. and J. H. Finucane (1991) Spatial distribution and abundance of ichthyoplankton, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. *Marine Ecology Progress Series*, **75**, 109–119.

Gunter G. (1979) The annual flows of the Mississippi River. *Gulf Research Reports*, **6**, 283–290.

Lam D. C. L., C. R. Murthy and R. B. Simpson (1984) *Effluent transport and diffusion models for the coastal zone*, Springer-Verlag, New York, 168 pp.

Lapicque G. and J. Ph. Breittmeyer (1973) Attempt to evaluate the extension in the area of pollution of river origin and application to some Mediterranean rivers. *Revue Internationale d'Oceanographie Medicale*, **30**, 61–87.

Lewis R. E. (1984) Circulation and mixing in estuary outflows. *Continental Shelf Research*, **3**, 201–214.

Luketina D. A. and J. Imberger (1989) Turbulence and entrainment in a buoyant surface plume. *Journal of Geophysical Research*, **94**, 12619–12636.

Murthy C. R. (1976) Horizontal diffusion characteristics in Lake Ontario. *Journal of Physical Oceanography*, **6**, 76–84.

Neilson J. D. and R. I. Perry (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? *Advances in Marine Biology*, **26**, 115–168.

O'Donnel J. (1990) The formation and fate of a river plume; a numerical model. *Journal of Physical Oceanography*, **20**, 551–569.

Okubo A. (1976) Remarks on the use of "diffusion diagrams" in modeling scale-dependent diffusion. *Deep-Sea Research*, **23**, 1213–1214.

Olson D. B. and R. H. Backus (1985) The concentrating of organisms at fronts: A cold-water fish and a warm-core Gulf stream ring. *Journal of Marine Research*, **43**, 113–137.

Sabatés A. (1990) Changes in the heterogeneity of mesoscale distribution patterns of larval fish associated with a shallow coastal haline front. *Estuarine Coastal and Shelf Science*, **30**, 131–140.

Shapiro S. S. and M. B. Wilk (1965) Analysis of variance test for normality (complete samples). *Biometrika*, **52**, 591–611.

Seim H. E., B. Kjerfve and J. E. Sneed (1987) Tides of Mississippi Sound and the adjacent continental shelf. *Estuarine Coastal and Shelf Science*, **25**, 143–156.

Simpson J. H. and I. D. James (1986) Coastal and estuarine fronts. In: *Baroclinic processes on continental shelves*, C. N. K. Mooers, editor, American Geophysical Union, Washington, pp. 63–93.

Wright L. D. and J. M. Coleman (1971) Effluent expansion and interfacial mixing in the presence of a salt wedge, Mississippi River Delta. *Journal of Geophysical Research*, **76**, 8649–8661.